Species Diversity, Regeneration and Early Growth of Sal Forests in Nepal: Responses to Inherent Disturbance Regimes

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Cover: Disturbances induced by wood collection (left), browsing (centre) and fodder collection (right) in Nepalese Sal forests.
(Photo: I. P. Sapkota)

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Abstract

Forest disturbance has been the subject of intense research for many years, but the synergistic effects of various disturbance factors on the forest vegetation are not well documented, particularly in Sal forests. In this thesis, the nexus between a bundle of inherent disturbances of varying intensities and the diversity and/or regeneration of Nepalese Sal forests was examined. In addition, the effects of a single disturbance factor – tree fall gaps – on species diversity, regeneration and early growth of Sal forest were assessed. The intensity of the combined inherent disturbances in each of the studied forest was calculated, and was found to have differing effects on various aspects of the forest vegetation. The total stem density of saplings and poles increased with increasing disturbance intensity, to a certain level, while most of the tree species in the community showed changing dispersion patterns along the disturbance gradient. Socially preferred tree species displayed high regeneration performance in forests subjected to moderate level of disturbance. Tree fall gaps favored regeneration by increasing the density of seedlings of some socially preferred tree species (including Sal) and promoted the maintenance of high species diversity. However, neither overall species diversity nor regeneration positively correlated with gap size, suggesting that the maintenance of species diversity and regeneration in gaps are related more strongly to several other attributes of gaps than gap size. Generally, forests subjected to moderate level of disturbance maintained species diversity and enhanced regeneration performance, which in turn was coupled with the regeneration strategy of dominant tree species – in line with the Intermediate Disturbance and Recruitment Limitation Hypotheses. In conclusion, the findings signify that moderate level of disturbance may be touted as a management tool for Sal forests.

Keywords: Canopy gaps, Forest disturbance, Intermediate disturbance hypothesis, Multiple disturbances, Recruitment limitation hypothesis, *Shorea robusta*

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Dedication

To my mother, the late Mrs. Dev Kumari Sapkota.

You passed away while I was struggling to finish this thesis.

Your wish to hug your graduated son remains unfulfilled. I am sorry mom!

You were the best mother in this entire world. I am really proud to be your son, and I wish you to give me birth again in the next incarnation.

I miss your lap every day!

Rest in heaven my dear mom!

मेरी प्यारी आमाको आत्माको चीर शान्तिको लागि म भगवानसंग प्रार्थना गर्दछु !!!

Contents

List of Publications

This thesis is based on the work presented in the following papers, which are referred to in the text by the corresponding Roman numerals.

I Indra Prasad Sapkota, Mulualem Tigabu, Per Christer Odén (2009). Spatial distribution, advanced regeneration and stand structure of Nepalese Sal (*Shorea robusta*) forests subject to disturbances of different intensities. *Forest Ecology and Management* 257(9), 1966-1975.

II Indra Prasad Sapkota, Mulualem Tigabu, Per Christer Odén (2010). Changes in tree species diversity and dominance across a disturbance gradient in Nepalese Sal (*Shorea robusta* Gaertn. f.) forests. *Journal of Forestry Research* 21(1) (in press).

III Indra Prasad Sapkota, Mulualem Tigabu, Per Christer Odén (2009). Species diversity and regeneration of old-growth seasonally dry *Shorea robusta* forests following gap formation. *Journal of Forestry Research* 20(1), 7-14.

IV Indra Prasad Sapkota, Per Christer Odén (2009). Gap characteristics and their effects on regeneration, dominance and early growth of woody species. *Journal of Plant Ecology* 2(1), 21-29.

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Papers not included in this thesis:

A. Indra Prasad Sapkota, Mulualem Tigabu, Per Christer Odén (2009). Tree diversity and regeneration of community-managed Bhabar lowland and Hill Sal forests in central region of Nepal. *Bois et Forêts des Tropiques* 63(300), 57-68.

B. Indra Prasad Sapkota, Per Christer Odén (2008). Household characteristics and forest dependency on community forests in Terai of Nepal. *International Journal of Social Forestry*1(2), 123-144.

The contribution of Indra Prasad Sapkota to each paper included in this thesis amounted to ca. 80% of the total work load.

'Man has been endowed with reason, with the power to create, so that he can add to what he's been given. But up to now he hasn't been a creator, only a destroyer. Forests keep disappearing, rivers dry up, wild lives become extinct, the climate ruined and the land grows poorer and uglier every day.' —Anton Chekhov

1 Introduction

1.1 General overview of Sal forests

1.1.1 Regional distribution and ecology of Sal forests

The Sal forest is one of the major forest types in South Asia characterized by the dominance of *Shorea robusta* Gaertn. f. Its geographic range extends from the southern slopes and lower foothills of the Himalayas to plains, river slopes and valleys in Nepal, Bangladesh, India, Bhutan and South China **(Fig. 1)**, between 75^{o} and 95^{o} E longitude and 20^{o} to 32^{o} N latitude (Gautam, 1990; Fu, 1994; Zhao *et al*., 1994; Gautam, 2001; Gautam & Devoe, 2006). Sal forests cover 0.12 million ha in Bangladesh (Alam *et al.*, 2008), 10.57 million ha in India (Rathore, 2000) and 1.4 million ha in Nepal (Rautiainen, 1999). These forests are generally located at altitudes from 100 m to 1700 m above sea level (Shankar, 2001; Gautam & Devoe, 2006), in zones that receive high precipitation ranging from 1000 to 3484 mm, with dry periods of between 4 and 6 months per year (Tewari, 1995; Shankar, 2001).

Depending on the degree of rainfall and soil moisture status, Sal forests can be either 'moist' or 'dry' (Champion & Seth, 1968a; Shankar, 2001). Moist Sal forests are confined to swampy areas, whereas dry Sal forests are confined to the relatively drier plateau regions (Chauhan, 2002). Dry Sal forests receive rainfall mainly during the wet period (May to October), and hence are termed 'seasonally dry' Sal forests (Shankar, 2001).

Sal tree grows in habitats with a wide range of soil types, but not on very sandy, gravely soils that immediately adjoin rivers or waterlogged areas (Jackson, 1994). It can grow on alluvial to lateritic soils (Tewari, 1995) and prefers slightly acidic to neutral sandy loam (pH = 5.1 – 6.8)

(Gangopadhyay & Banerjee, 1987; Rana, Singh & Singh, 1988; Gangopadhyay *et al.*, 1990).

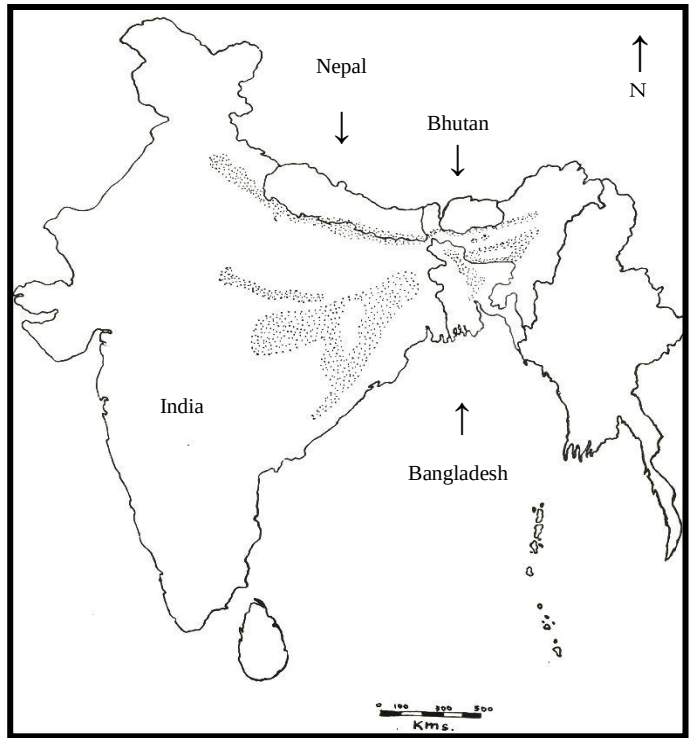


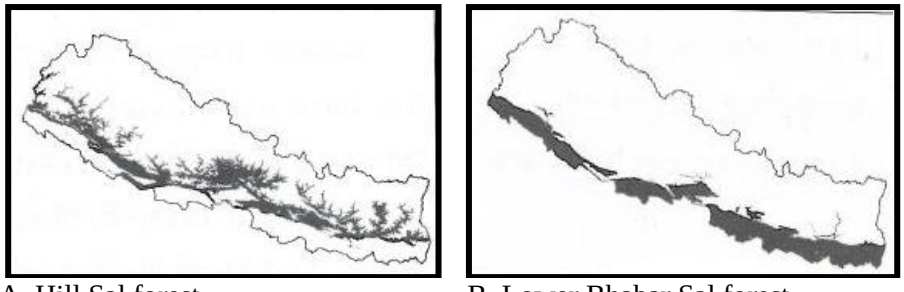
Figure 1. Distribution of Sal forests (dotted areas) in South Asia (Anon., 1985)

Since Sal forests consist of many tree and shrub species in different layers, the phenology of the Sal stands interacts with the phenology of these species. Leaf fall usually starts in late winter (Misra, 1969) and peaks between mid-February and mid-May (Pokhriyal, Ramola & Raturi, 1987; Singh, Sharma & Rawat, 1993).

1.1.2 Nepalese Sal forests and stand attributes

Sal forests in Nepal are broadly classified into two types: Hill Sal forests and lower tropical or mixed broadleaved Sal forests (Stainton, 1972; Anon., 2002) **(Fig. 2)**. Hill Sal forests include upper tropical forests (Anon., 2002), tropical and sub-tropical forests (Stainton, 1972) and northern tropical dry deciduous forests (Champion & Seth, 1968b). They are dominated by *S. robusta*, together with other broadleaved trees, such as *Lagerstroemia*

parviflora Roxb., *Anogeissus latifolia* (Roxb. Ex DC.) Wall. and *Adina cardifolia* (Roxb.) Hook. f. Ex Brandis. In contrast, the lower tropical Sal forests, also known as lower Bhabar Sal forests, do not have many associates and Sal tends to dominate the entire vegetation cover over *Terminalia alata* Heyne ex Roth., *Terminalia bellirica* (Gaertn.) Roxb., *Terminalia chebula* Retz., *Syzygium cumini* L. Skeels. and some of the above mentioned species (Anon., 2002). The Sal forest types in Nepal are further classified into different ecotypes (i.e. dry, moist or wet) depending on the climatic, edaphic, and biotic conditions; with varying species association and density as well as a stratified height structure (Gautam & Devoe, 2006).



A. Hill Sal forest B. Lower Bhabar Sal forest

Figure 2. Distributions of the major Sal forest types in Nepal (Hill and Lower Bhabar, shaded areas) (Anon., 2002)

Sal trees in lower tropical forests grow to a considerable size, while they are typically much smaller in the Hill Sal forests. Sal trees can grow up to 40 m in height, whereas other emergent tree species normally reach 35 m (Gautam & Devoe, 2006). Most of the regeneration stock in Sal-dominated mixed forests normally originates from re-sprouting through root suckers (Suoheimo, 1999). Sal forests are relatively rich in floral diversity (Gautam & Devoe, 2006). Besides trees and shrubs, the ground flora of Sal forests comprises ferns, herbs, grasses and liana species (Maithani, Sharma & Bahuguna, 1989; Gautam & Devoe, 2006), which vary in abundance between different forests.

1.2 Degradation and current management of Nepalese Sal forests

Sal forests in the Bhabar lowland (Terai plains) of southern Nepal remained intact with large well-preserved forest areas until the 1960s. Following a

malaria eradication program and associated resettlement policy, a major forest invasion by landless people caused rapid forest degradation. The reduced fear of contracting malaria brought more people from the hilly areas to the lowlands, which over time saw further deforestation as a result of increases in internal migration, and a 5% rise in population growth rate (Suoheimo, 1999). Approximately six million tons of fuel-wood is extracted annually, and ca. 70% of the total national energy consumption is met by wood from these forests. Sal trees are extensively used for timber production due to the high value of Sal timber (Gautam & Devoe, 2006). A diversity of other products, such as fodder, fuel-wood, animal bedding materials, leaf litter, timber and a number of other NTFPs (Webb & Sah, 2003; Gautam & Devoe, 2006), has also been removed from Sal forests. Hence, these forests are subjected to high anthropogenic disturbances as more than 80% of the rural population of Nepal depends on such forests to meet their subsistence needs. Consequently, there is a continuing loss of forest cover amounting to approximately 1.3% per annum (Suoheimo, 1999). Estimates indicate that the Sal forests in the Terai are not able to meet the rising local pressure for fuel-wood and timber (Suoheimo, 1999) unless the remaining forests are managed in a sustainable way. Hitherto the only management practice is a selection system based on 'high grading', in which the trees removed are mostly of large and/or dead, dying and diseased. This management system is considered to be partly responsible for the degradation of Sal forests in Nepal, which has influenced the entire forest area and been a major factor shaping the current residual forest structure (Suoheimo, 1999).

1.3 Disturbance and ecosystems: a theoretical perspective

Disturbance is generally defined as any relatively discrete event in time that disrupts an ecosystem, community, or population structure and changes resource pools, substrate availability or the physical environment (White & Pickett, 1985). Disturbance may be natural or have an anthropogenic origin (Turner *et al.*, 2003) and may lead to sudden or gradual, dramatic or subtle changes in ecosystems (White & Jentsch, 2001). Disturbances are ubiquitous, inherent (inbuilt), unavoidable and affect all levels of biological organization from individuals to ecosystems and landscapes with different consequences and mechanisms at each hierarchical level (Rykiel, 1985). An inherent disturbance is a type of disturbance integral to a given forest ecosystem (Perera & Buse, 2004), which can be autogenic (arising from within) and allogenic (arising from outside the system).

The effects of disturbances often depend on the frequency, intensity and timing of their interactions, on the past and present states of the system and their interaction with future events (Frost *et al.*, 1986). Disturbances are the primary causes of patchiness and heterogeneity in ecosystems (Turner *et al.*, 2003) and are evolutionary forces that shape the adaptation of biota exposed to them (McNaughton, 1983; Langevelde *et al.*, 2003). Disturbance exerts diverse effects on ecosystems (Arnold & Ruiz Perez, 2001), which can cause various ecosystem characteristics to either rise or fall beyond their normal ranges (Godron & Forman, 1983). The changes caused by disturbance can vary from negligible to extreme, depending on the intensity of the disturbance itself and the vulnerability of the target organisms or the system (Sousa, 1984). Disturbance can cause long-term and short-term changes in habitats, with direct and indirect effects on populations (Sousa, 1984). A disturbance may change factors such as nutrient levels, light regimes, substrate types, and dominance patterns. Following a disturbance, some species may increase in abundance or invade, while other species may decline or retreat (Gibson & Brown, 1991; Jonsson, 1993). Such functional adaptations underlie two mechanisms of ecosystem response to disturbance, complementarity and redundancy (Walker, 1992), which contribute to ecosystem resilience.

Two hypotheses – the Intermediate Disturbance Hypothesis (IDH) (Connell, 1978; Sheil, 1999; Van Der Meer, Sterck & Bongers, 1998; Milino & Sabatier, 2001; Sheil & Burslem, 2003; Roxburgh, Shea & Wilson, 2004; Johst & Huth, 2005) and the dispersal or recruitment limitation hypothesis (Hurtt & Pacala, 1995; Chazdon *et al.*, 1999; Hubbell, 1999; Hubbell *et al.*, 1999) – have often been used to explain the mechanisms involved in the maintenance of tree species diversity and its components in disturbed forest ecosystems (Koehler & Huth, 2007). According to IDH, too much disturbance leads to the loss of late successional species, whereas too little leads to the exclusion of species adapted to colonize ecosystems immediately after disturbance (Sheil & Burslem, 2003). Therefore, an intermediate disturbance regimes enables community co-existence (Molino & Sabatier, 2001; Sheil & Burslem, 2003). On the other hand, the second hypothesis states that dispersal or recruitment limitations normally outweigh the role of an intermediate disturbance regimes. It emphasizes that although disturbances in mature forests increase the choices of available niches, these would not necessarily be filled by the most adapted species, but rather by species whose propagules are sufficiently abundant at the right time and at the right place (Hubbell *et al.*, 1999). Nevertheless, both hypotheses indicate that disturbance can have both positive and negative impacts on ecosystems and plant communities (Sousa, 1984), highlighting the importance of

understanding these phenomenon for formulating ecologically founded ecosystem management strategy (Turner *et al.*, 2003).

1.3.1 Conceptual framework for the studies

Based on current theoretical and empirical understandings of forest disturbance, a conceptual framework for the study was formulated (**Fig. 3)**. It is presumed that major inherent (or inbuilt) disturbance regimes have both positive and negative impacts on Sal forest ecosystems, depending on their intensity and frequency. It is also assumed that other factors (such as climate, soil and fire) are associated with alterations of ecosystems, thus are constantly placed in the background to ensure that research designs are appropriate, and that inferences drawn are generally applicable to all Sal forests in Nepal.

The resilience of Sal forest ecosystems are generally believed to be reflected in the status and trends of features and processes of the systems, such as regeneration, species diversity, population structure, species spatial pattern, community dominance, species composition and early growth of regenerating species of the forest community. These ecosystem characteristics often change over time as successional changes occur in the system (De Leo & Levin, 1997). However, several sources of disturbance, such as selective felling, natural plant death, grazing and browsing by herbivores, and collection of wood and non-wood products by locals inevitably occur in the Sal forest ecosystems, and are often considered to be key determinants of ecosystem resilience. In addition, fire regimes, climate variability and soil conditions influence the resilience of a forest ecosystem; however these factors are of minor importance in the current study. Because no fire effect was observed during the field assessment, while the soil and climatic conditions are similar among the studied forests. The likely effect of different forest management regimes in each Sal forest is mingled with their use patterns, which in turn was the basis for quantifying the disturbance magnitude.

The conceptual framework further presumes that although the resilience of Sal forest ecosystems is often affected by single, specific, inherent (or inbuilt) sources of disturbance, the simultaneous occurrence of several types of disturbance, if exerted in a bundle, will cause even stronger and more practically important changes in status and trend (negative in some cases and positive in others) of various ecosystem characteristics. The effects of interactions between and/or among the individual disturbance factors, which cause either positive or negative changes to a number of parameters of forest ecosystems (e.g. forest dynamics, species composition,

diversity and early growth) are also likely to occur. Consequently, these changes in ecosystem characteristics determine whether or not disturbance will promote or inhibit the resilience of forest ecosystems. The disturbance-ecosystem resilience nexus that the proposed conceptual framework is based upon is reviewed thoroughly below.

1.3.2 Herbivory

Herbivory by wild animals (autogenic disturbance) and livestock (allogenic disturbance) are inherent disturbance in Sal forests (**Fig. 3**), and cause positive or negative effects on structure and function of forest ecosystem, depending on their intensity (Van Wyk & Fairall, 1969; Abdel-Magid, Trlica & Hart, 1987; Hiernaux *et al.*, 1999; Harris, 2002; Cumming & Cumming, 2003; Rufino *et al.*, 2006; Pradhan, Wegge & Moe, 2007). The primary and most obvious effect of herbivores is the removal of biomass through browsing and grazing, which is the main biotic factor affecting vegetation structure and dynamics (Belsky, 1992; Milchunas & Lauenroth, 1993; Díaz, Noy-Meir & Cabido, 2001; Bakker *et al.*, 2006). Herbivores hinder the regeneration process through seed and seedling consumption (Bullock, 2000; Drexhage & Colin, 2003; Zida, 2007), and by exacerbating drought via soil compaction, which in turn reduces soil infiltration (Kozlowski, 1999; Savadogo, 2007; Savadogo, Sawadogo & Tiveau, 2007). Heavy browsing also suppresses the height growth of seedlings and saplings (Beguin, Pothier & Prevost, 2009; Dharani *et al*., 2009). Overgrazing leads to the degradation of plant and soil resources (Keya, 1998) and the loss of species richness, while favoring the abundance of unpalatable species (Mwendera & Saleem, 1997; Beguin, Pothier & Prevost, 2009). Mega herbivores (e.g. Elephants) disturb the forests through uprooting and debarking of trees (Pradhan, Wegge & Moe, 2007).

In contrast, herbivores enhance the colonization process through the long distance dispersal of seeds (Miller, 1995; Jordano, 2000; Stiles, 2000), facilitate seed germination through gut action (Traveset, 1998; Traveset & Verdú, 2002; Razanamandranto *et al.*, 2004) and regulate tree-grass competition (Scholes & Archer, 1997). In addition, grazing regulates the competition between woody plants and grasses for light, water and nutrients, thereby promoting co-existence via ‘facilitation mechanisms’ (Scholes & Archer, 1997), and browsing helps the herbaceous layer to produce biomass as well as to maintain species composition (Scholes & Walker, 1993; Scholes & Archer, 1997).

1.3.3 Plant death and selective logging

Plant deaths from natural causes, such as pests and pathogens, harsh climatic conditions (autogenic inherent disturbances) and selective removal of trees (allogenic inherent disturbance) influence either positively or negatively the structure and function of forest ecosystems (Denslow, 1980; Bradshaw & Goldberg, 1989; Bullock, 2000). Generally, canopy gaps created by death and/or selective logging of trees are expected to result in increased diversity and abundance due to reduced competition for water and nutrients, together with increases in the availability of light (Frost *et al.*, 1986) and soil temperature (Bullock, 2000). The gaps may create suitable conditions for the germination of seeds in soil seed banks and seed rains, thereby facilitating the colonization process (Bullock, 2000). The rates of emergence and survival of seedlings increase with increases in the number and size of canopy gaps (Bullock, 2000; Hutchinson, Sutherland & Yaussy, 2005; Vandenberghe *et al.*, 2006), especially when light and temperature are growth limiting factors. Further, for many tree species, gaps encourage both sexual and asexual reproduction by promoting not only seed germination (Teketay & Granström, 1997; Bullock, 2000; Yirdaw & Leinonen, 2002; Yirdaw & Luukkanen, 2004) but also the development of coppices and/or root suckers (Pande, 1999; Sawadogo, Nygård & Pallo, 2002; Ky-Dembele *et al*., 2007; Sapkota, Tigabu & Odén, 2009). In response to the loss of foliage or stems, many plants resprout (coppice) either along the remaining stems or from the root stock (Kammesheidt, 1998; Paciorek *et al.*, 2000; Bond & Midgley, 2001; Ky-Dembele *et al.*, 2007). At the community level, this phenomenon has been considered to be more effective mode of stand regeneration than regeneration by seeds (Mwavu & Witkowski, 2008; Ky-Dembele *et al*., 2007), in large part due to the higher chance of survival and rapid growth of such sprouts (Winkler & Fischer, 2001; Mwavu & Witkowski, 2008). The prevalence of re-sprouting among forest species (Murphy & Lugo, 1986) can help forests recover to mature state more quickly and assure persistence of species that readily resprout in forest communities (Mwavu & Witkowski, 2008). Thus, forests that host such species are more resilient than forests in which there are no such species (Ewel, 1977; Mwavu & Witkowski, 2008).

In contrast, gaps created by the selective removal of trees in moisture-limited environments may hinder seed germination and seedling establishment due to reductions in surface soil moisture and consequent depletion of water resources exacerbated by higher light intensities

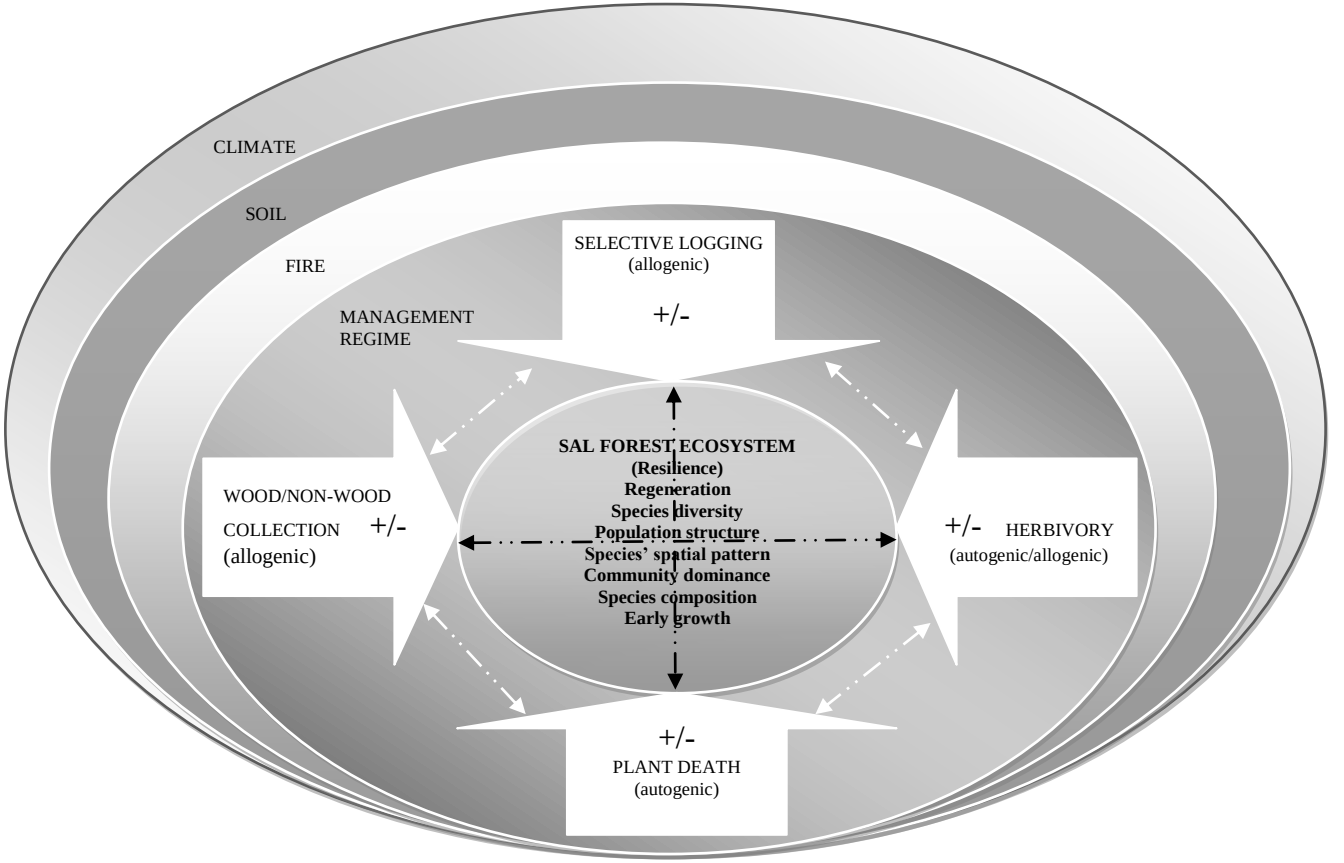


Figure 3. A simplified conceptual framework describing positive and negative effects of autogenic and allogenic inherent disturbances on the resilience of Sal forests. Factors, such as climate, soil, fire and forest management regimes potentially influence the response of the ecosystem.

(Denslow, 1980; Collins, Dunne & Pickett, 1985; Vitousek & Denslow, 1986; Bradshaw & Goldberg, 1989; Aguilera & Lauenroth, 1995) and increases in soil temperatures (Olvera-Carrillo *et al.*, 2009). Selective removal of reproductively mature trees may result in paucity of seed availability, thus leading to poor stand regeneration, as availability of remnant mature trees has widely been shown to be the foci of regeneration in disturbed sites (Guariguata & Ostertag, 2001; Castro-Marín *et al.*, 2009; González-Rivas *et al.*, 2009). Moreover, the changes in resource availability and environmental conditions following selective tree cutting generally result in immediate increases in the herbaceous layer (Scholes & Walker, 1993; Gambiza *et al.*, 2000), which lead to severe competition with tree regeneration.

1.3.4 Wood and non-wood collection

The exploitation of wood and non-wood forest products (fuel-wood, fodder, litter, bedding materials for animals, and several other NTFPs) by the local people (allogenic inherent disturbance) has varying positive or negative effects on forest ecosystems, depending on the type of species and the parts being harvested (Arnold & Ruiz Perez, 2001). For example, lopping for fodder and fuel-wood (Melkania & Ramnarayan, 1998; Jashimuddin, 1999; Rawat & Bhainsora, 1999) has been viewed as the most significant activity inhibiting forest regeneration in the region (Saxena & Singh, 1984), reducing tree vigor as well as seed production (Saxena & Singh, 1984; Gautam, 2001). Since seed output is reduced by lopping, the pressure of biotic agents on the remaining seed crop increases, in turn reducing the viable seed population (Sagar & Singh, 2004). During fodder collection, lopping events are often concentrated on a single species, which causes the entire structure of the plant community to change (Spurr & Barnes, 1980). Litter collection (removal of dead leaves) from the forest floor drains nutrients from the system and reduces fertility (Schmidt, Schreier & Shah, 1993; Melkania & Ramnarayan, 1998).

In contrast, foliage removal through lopping events decreases ground litter, which is known to create mechanical hindrance for seed germination and seedling establishment (Champion & Osmaston, 1962; Troup, 1986). Lopping increases the availability of light in the forest floor and the surface temperature (Molofsky & Augspurger, 1992), which have been shown to inhibit the germination of seeds of some plants, e.g., *Opuntia tomentosa* Salm-Dyck. (Olvera-Carrillo *et al.*, 2009) and the Australian genus *Frankenia* L. (Easton & Kleindorfer, 2008). Kumar, Singh, & Abbas (1994) and De Cássia Guimarães Mesquita (2000) provided further evidence that lopping for fodder and litter collection enhances the

regeneration of many species. Lopping and litter collection in forests can also have either negative or positive effects on fungal pathogens (Rotem, 1978; Gautam, 2001) and the photosynthetic rates of individuals, consequently affecting the growth rate of plant communities (McGraw *et al.*, 1990; Gautam, 2001).

1.3.5 Interaction among disturbance factors

Disturbances in ecosystems not only act independently but also interactively (Belsky, 1992; Valone, Nordell & Ernest, 2002; Valone, 2003). Generally, the co-occurrence of a number of disturbance factors has a synergistic effect on forest ecosystem both in time and space (McNaughton, 1983). For example, selective cutting and/or plant death temporarily provides more space and resources for the growth of herbaceous species (Wiegand, Saitz & Ward, 2006), which in turn attracts the herbivores. Selective cutting may also favor the dominance of drought-tolerant species (e.g. shrubs and herbs) while grazing may reduce their abundance. Similarly, wood and non-wood collectors cause plant death and leave branches and foliage in the site that can attract more herbivores. Herbivores may graze the herbaceous layer as well as browse seedlings and saplings causing plant death at both layers. Felling damage occurring on remaining stands may create conditions favorable for pathogenic and insect impacts, thus may trigger tree death. Increasing tree death by natural or man-made causes attracts more wood collectors. Selective logging of reproductively mature trees and herbivory reduce the availability of fruits and seeds, thereby hindering stand regeneration. Thus, the interactive effects of these factors influence the resilience of a forest ecosystem in either positive or negative way, depending on their severity.

1.4 Relevance of disturbance studies in Sal forests

The residual structure of Sal forests is the consequence of actions and interactions of biotic and abiotic disturbances (Gautam & Devoe, 2006) that have either natural or anthropogenic origin. Natural disturbances, such as seasonal windthrow of trees (due to root decay) and loosening of footholds in the soil have been observed in the Sal forests (Maithani, Sharma & Bahuguna, 1989). In addition, these forests are preferred habitat for many wildlife species that have damaged the forests (Pradhan, Wegge & Moe, 2007). As a result, forest trees are frequently injured and the soil is disrupted from its original state (Maithani, Sharma & Bahuguna, 1989). Anthropogenic disturbances such as selective logging and illicit felling

have been widely practiced since the inception of the timber and fuel-wood trade in the region (Sapkota, Tigabu & Odén, 2009). Increasing rural demand for leaf fodder has increased grazing and browsing pressure in the forests. Cutting and lopping for fuel-wood and fodder, and the collection of ground litter for livestock feed and bedding materials have occurred widely in Sal forests (Melkania & Ramnarayan, 1998; Jashimuddin, 1999; Rawat & Bhainsora, 1999). Several non-timber forest products (NTFPs) (Dwivedi, 1993; Edwards, 1996; Rao & Singh, 1996; Sah, 1996; Melkania & Ramnarayan, 1998; Webb & Sah, 2003) including Sal seeds (Maithani, Sharma & Bahuguna, 1989) have frequently been collected to support the livelihoods of local people (Gautam & Devoe, 2006). Such diverse uses of Sal forests coupled with natural disturbances signify that these forests are exceptionally disturbed (see photo plate). Disturbances are something that cannot be avoided in Sal forests, but rather are something to deal with. For this, multiple disturbances occurring in Sal forests need to be thoroughly studied, and their impacts on ecosystem resilience have to be extensively assessed. Unfortunately, systematic investigation of the disturbance-forest ecosystem resilience nexus in Nepalese Sal forests is scanty.

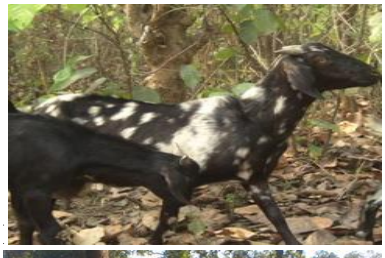
Most studies in Sal forests of Nepal have mainly focused on the community analysis of protected and/or natural forests (e.g. Webb & Sah, 2003; Timilsina, Ross & Heinen, 2007), natural regeneration and seedling growth following regeneration felling (e.g. Rautiainen & Suoheimo, 1997; Suoheimo, 1999), yield optimization (e.g. Rautiainen, 1999), impact of different management regimes on stand structure (e.g. Webb & Sah, 2003) etc. Few studies related to single disturbance factor such as herbivory (e. g. Pradhan, Wegge & Moe, 2007) and lopping regimes (e.g. Gautam, 2001) have also been made. But these studies have also left ample rooms for studying how multiple disturbances actually influence the Sal forest ecosystems.

Since the inception of participatory forest management and conservation concept in Nepal in 1970s, the forest policies vow an ecosystem-based forest management regimes (Gautam & Devoe, 2006), i.e. a practice of managing forest ecosystems in ways that are compatible with both ecological processes and societal needs and/or forest use patterns (Oliver & Larson, 1996). Knowledge of the forest disturbances (in terms of their types, nature and/or sources) that occur in Sal forest ecosystems and their relationships with diversity, regeneration and early growth of woody species (ecosystem integrities) is the foundation for developing such ecosystem-based forest management regimes. Elucidation of the relationships between disturbance and ecosystem characteristics needs a

Current disturbances

Current vegetation status

I



II

III

IV

V

Photo plate: Examples of current disturbances in Sal forests and corresponding vegetation change. The Roman numerals indicate the disturbance gradient from least (I) to heavily disturbed (V).

holistic approach in such a way that the synergistic effects of all possible sources of forest disturbances (hereafter referred to as bundle of disturbances) occurring simultaneously on the Sal forest ecosystem are studied.

Studying the synergistic effects of the bundle of disturbances gives a complete picture of forest ecosystem response to inherent disturbances. This approach is necessitated because several disturbance sources (e.g. harvesting, cutting, lopping, breakage, browsing, uprooting etc.) are operating simultaneously in nature and driving the forest vegetation change collectively. Any study, which disregards each simultaneous disturbance factor, may potentially mask the factual inferences. Thus, the first two studies of this thesis examined the synergistic effects of a bundle of disturbances on regeneration, stand structure, dispersion and diversity of Sal forests. Such an approach has already been employed to examine the synergistic effects of several disturbance factors on species composition, dispersion and diversity of tropical dry forests of India (Sagar et al., 2003). In addition, the first study also examined how a bundle of disturbances influences the regeneration performance of socially preferred species in the region.

Regeneration and diversity following gap creation by selective logging, a common management practice in the Nepalese Sal forests, and/or natural tree fall have not been the subjects of scientific research in the past. Understandings of the responses of stand-level species diversity and regeneration to the gaps, and their relationships with gap attributes are very crucial in optimizing the forest management practices in one hand, and expediting the forest recovery process on the other. Thus, the second two studies reported in this thesis examined individual responses of species diversity and regeneration to the gap, assessed the gap attributes and elucidated how they influence the stand-level regeneration, diversity and early growth of Sal forests. In addition, the third study also examined the responses of regeneration performance of socially preferred species to the gaps. As a whole, the findings will hopefully contribute to filling the gaps in our knowledge of disturbance dynamics in Sal forests and ecosystem resilience.

'Earth provides enough to satisfy every man's need, but not any man's greed.' — Mahatma Gandhi

2 Objectives and hypotheses of the studies

The general objective of the studies was to elucidate the relationships between small-scaled (but frequent) fluctuating disturbances of an inherent (or inbuilt) nature and diversity, regeneration and early growth of woody species, in order to facilitate the design of a multiple use management system for Sal forests, and to enhance the regeneration performance of locally preferred tree species. Hence, in the studies, a number of indicators of diversity, regeneration and early growth of woody species were used to assess ecosystem responses to disturbance regimes of various types and magnitudes in Sal forests.

Specific objectives of the studies were:

1. To examine the changes in stand structure, spatial dispersion, stand level regeneration and regeneration of socially preferred species of Sal forests across a disturbance gradient (Study I)

2. To assess the changes in species diversity, species importance and community dominance across a disturbance gradient (Study II)

3. To examine the responses of stand-level species diversity and regeneration, and the regeneration of socially preferred tree species to a single disturbance factor – the tree fall (Study III)

4. To characterize gap attributes and assess their impacts on species diversity, community dominance and early growth of woody species (Studies III and IV)

Hypotheses tested:

1. Stand structure, spatial dispersion and regeneration of tree species vary among disturbed Sal forests, and the variation is related with the intensity of a bundle of inherent disturbances.

2. Tree species diversity and community dominance vary among disturbed Sal forests, and the variation is related with the intensity of a bundle of inherent disturbances.

3. Tree fall gap (single inherent disturbance factor) enhances species diversity and regeneration of Sal forests.

4. Regeneration, diversity, community dominance and early growth of Sal forests are associated with tree fall gap attributes.

'The goal of life is living in agreement with nature.' —Zeno

3 Materials and Methods

3.1 Research sites

Five seasonally dry deciduous Sal forests managed in three different ways – as community managed forests (CFs), buffer zone forests (BZFs) and state managed forests (SMFs) – representing climatic vegetation were selected for the studies (Anon., 1994; Webb & Sah, 2003). These forests are located in the Nawalparansi district of Nepal at 27° 24' - 27° 52' N latitude and 83° 34' - 84° 26' E longitude **(Fig. 4)**. Management responsibilities and ownership have been recently assigned to the local community in the CFs and BZFs (forest areas between settlements and the core protected forests), while the government owns and manages the entire forests in the SMF. All five forests were considered in studies I and II, while one of the largest areas of forest, Chisapani Danda SMF, was chosen for studies III and IV. All forests are growing on an alluvial plain with similar geological characteristics to the Gangetic plain of India to the south, while the underlying sediments originate from tertiary Siwalik material in the north (Anon., 1994). The Siwalik hills are composed of coarsely bedded stones, crystalline rocks, clays and conglomerates. The elevation of the forests sampled ranges from 105 m to 360 m above sea level. The texture of the soil (0-10 cm depth) varies from sandy to loam, while the ranges of pH and soil moisture are 5.2-6.3 and 6.3-11.7%, respectively. The climate in the area is tropical to sub-tropical. A typical year can be divided into three main seasons: cold, hot and rainy. May and June have the highest mean maximum temperatures (34.6^{o}C in both cases), while the coldest months are December and January (9.9^{o}C). Maximum rainfall occurs during the monsoon season (June-September), with an average monthly rainfall of 531.3 mm. Dew falls from December to February **(**see climatic data presented in **Fig. 5)**.

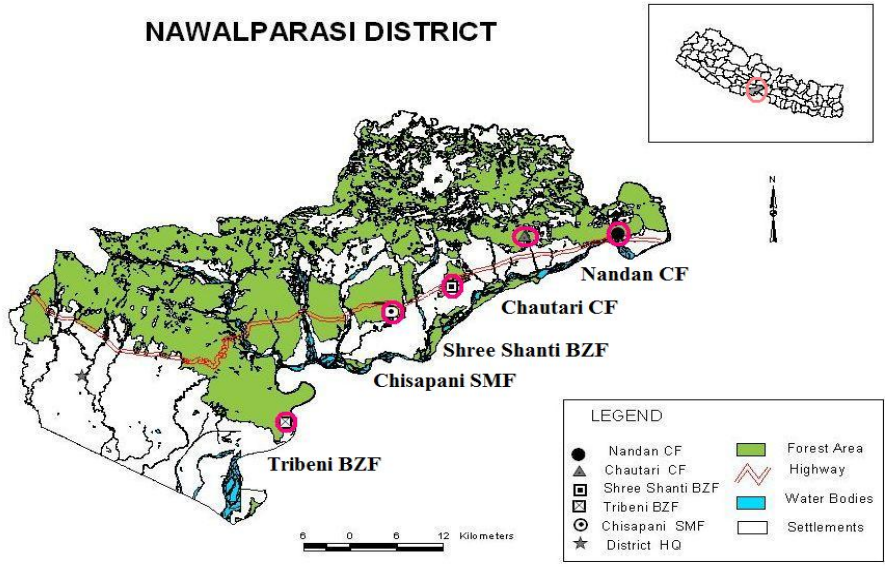


Figure 4. Locations of the five seasonally dry deciduous Sal forests.

Prior to 1963, the forests in the study area were nearly 'pristine' with high faunal and floral diversity. Later, malarial eradication programs, the construction of the East-West national highway and political unrest reduced the forest cover considerably. The continuous flow of migrating people from the hills to these lowland areas has caused further forest degradation and encroachment.

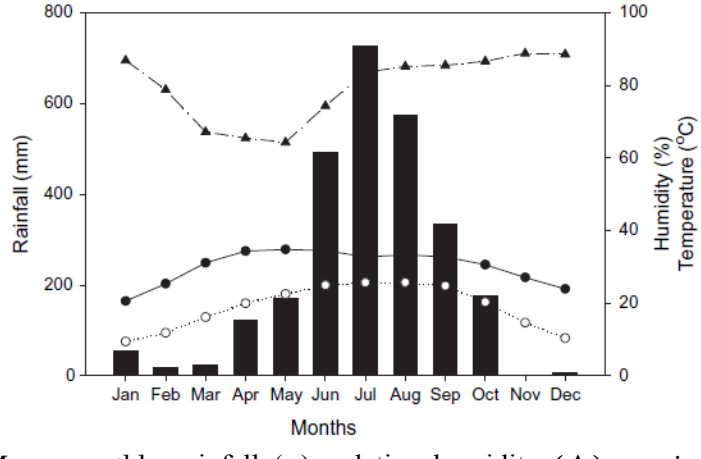


Figure 5. Mean monthly rainfall (■), relative humidity (▲), maximum temperature (●) and minimum temperature (○) of the study area (mean of years 2003-2005).

According to the forest management plan for this region (Anon., 1994), the annual deforestation rate between 1964 and 1990 was 2-2.4%. In this 25-year period, approximately half of the forest area in the district was either degraded or converted to other land uses.

3.2 Methods (Studies I & II)

In these studies the spatial pattern, stand structure, species diversity and advanced regeneration of important tree species subject to a bundle of disturbances of different intensities were investigated, and changes in their patterns across a disturbance gradient were examined.

3.2.1 Assessment of the bundle of disturbances

Prior to the inventory, all types, sources and indicators of disturbance that were deemed likely to have had significant effects in the forests were identified and their severity was assessed. Major sources or indicators of inherent disturbances that appeared to occur in a frequent and fluctuating manner and showed multiple and simultaneous effects on the forest vegetation, were considered. The most apparent signs of disturbances in the forests were plants damaged by windthrow, harvesting, cutting, lopping, breakage, browsing, uprooting, and/or damage associated with crown openness, clearance of footpaths and cart trails, animal feces and soil disturbed by several animal activities (e.g. wallowing, rooting and digging etc.). No major fire disturbances have been observed in these forests so such potential disturbances were not considered in these studies.

3.2.2 Sampling and inventory

A constant azimuth was chosen, and a transect line was laid out along it, in each of the five forests **(**at 40^{o}, 360^{o}, 20^{o}, 300^{o}, and 320^{o} for the five forests located from north east to south west of the district, respectively as shown in **Fig. 4)**. Using satellite images, each azimuth for each forest was set towards the forest core zone from corresponding settlements. Five 1-ha plots were established along the right-hand side of each transect at a successive interval of 200 m from the settlements. Each 1-ha plot was then divided into 25 sub-plots (each 20 m × 20 m) for sampling individuals with >20 cm diameter at breast height (dbh). A square quadrat of 25 m^2 was also laid out at the left corner of each sub-plot for sampling individuals of tree species with 1.5-20 cm dbh. The dbh of each individual was measured using digital calipers and a diameter tape (when possible). Based on the dbh

of each individual, the tree species were grouped into three categories: saplings (1.5-10 cm dbh), poles (> 10-20 cm dbh) and trees (> 20 cm dbh).

All individuals showing signs of damage in each sub-plot and quadrat were identified, counted and their collar diameters were measured. 'Time since disturbance' was estimated and categorized as 'recent' (< 2 years), 'old' (> 2 years to < 10 years) or 'very old' (> 10 years). This category was based on visual inspection of the bark, stem and leaf residues around the stumps, stump freshness, stump color, termite mounds and cracks in the remaining stumps. Crown openness was estimated using a densiometer. Disturbance by herbivores was estimated by counting the number of spots disturbed by wallowing, rooting and/or digging (e.g. by rhinos, wild pigs, deer, rodents, hedgehogs etc.) and animal feces (as indicators of their presence). Footpaths and trails were measured using a linear tape.

3.2.3 Assessment of disturbance impact factors

A modified method of Sagar, Raghubanshi & Singh (2003) was used to estimate a disturbance impact factor (DIF). The DIF was derived from the relative impact of major disturbance sources or indicators for each forest. DIF values for browsing, cutting, lopping, breaking and uprooting were obtained from estimates of the relative density and basal area of damaged individuals, defined as the ratio of total density and basal area of damaged seedlings, saplings, poles and trees to their total (damaged and non-damaged) density and basal area in each forest. The forests with the lowest values were assigned an impact factor of 1.0 for each disturbance indicator.

For other forests, the relative impact factor was calculated as the ratio of the relative density and basal area of disturbed individuals in respective forests to that of the forest with the lowest value. The impact factor was calculated according to 'time since disturbance' for each disturbance indicators. The relative impact factor of other disturbance indicator (crown openness, herbivory and footpath/trails etc.) was also estimated by assigning a value of 1.0 to the forest with the lowest number of cases and proportionally higher values to the other forests. Finally, the impact factors for each disturbance source or indicator were summed, and the forests were placed along a disturbance gradient from I (least disturbed) to V (heavily disturbed) **(Table 1)**.

Table 1. Relative impact factor for a bundle of disturbances and estimated disturbance impact factors (DIF) for each forest represented in this study.

A bundle of disturbances	Forests				
	Shusta Triveni	Chautari	Nandan	Chisapani	Shree Shanti
Browsing etc. (seedling density)	1	4	6	5.9	5.5
Lopping etc. (sapling/pole density)*	2.6	6.4	13.8	8.8	23
Lopping etc. (sapling/pole stump basal area)*	2.5	4.5	18.4	9.9	9.4
Harvesting etc. (adult tree density)*	3	7.1	7	16	8.7
Harvesting etc. (adult tree stump basal area)*	3	6	8.2	25.8	10.9
Crown openness	1	1.2	1.3	1.4	1.2
Wildlife and herbivores	14.1	15.7	3.5	1	32.8
Footpaths and trails	1	31.6	30.1	34.3	64.4
Animal feces	1	3.7	2.3	1.3	5.1
Total	29.2	80.2	90.6	104.4	161
Disturbance category/gradient	I	II	III	IV	V

* To take account of the additive effects of 'time since disturbance', the impact factor for these disturbance sources was first computed for recent, old and very old groups separately and then summed.

3.2.4 Data analysis

Curve estimation was performed to examine the relationships between DIF (x variable) and stand density, advanced regeneration/pole density of *S. robusta*, and the frequency of occurrence of *S. robusta* in quadrats (y variables). Regression was also performed to examine the relationships between stand density (y) and diameter class (x).

Dispersion patterns of species were characterized by calculating standardized Morisita's Index (Krebs, 1999) for each species in each forest in which ≥ 5 individuals of the species were detected in at least two of five 1-ha sampling plots. To do this, the Morisita's index of dispersion (I_d) was first calculated along with its two critical values, the uniform index (M_u) and the clumped index (M_c) as follows:

$$I_d = n\,[(\sum x^2 - \sum x) / (\sum x)^2 - \sum x]$$
$$M_u = (\chi^2_{0.975} - n + \sum x) / (\sum x) - 1$$
$$M_c = (\chi^2_{0.025} - n + \sum x) / (\sum x) - 1$$

where n is the sample size (5 × one-ha plots), x is the number of individuals, $\chi^2_{0.025}$ and $\chi^2_{0.975}$ are the values of chi-squared with (n-1) degrees of freedom that have 2.5% or 97.5% of the area to the right. The Standardized Morisita's index (I_p) was then calculated by one of the four following formulae:

1. $I_p = 0.5 + 0.5\,(I_d - M_c) / (n - M_c)$; when $I_d \geq M_c > 1.0$
2. $I_p = 0.5\,(I_d - 1) / (M_u - 1)$; when $M_c \geq I_d > 1.0$
3. $I_p = -0.5\,(I_d - 1) / (M_u - 1)$; when $1.0 > I_d > M_u$
4. $I_p = -0.5 + 0.5\,(I_d - M_u) / M_u$; when $1.0 > M_u > I_d$

I_p values range from -1 to +1. A value of zero indicates a random dispersion pattern, a value higher than zero indicates a clumped pattern, and a value below zero indicates a uniform pattern.

A pair-wise Mann-Whitney *U* test was performed to compare the density of saplings and poles of important species among forests.

Several diversity indices (Number of species, Margalef's index of species richness, Shannon-wiener index, Simpson's index) were also calculated for each plot in order to permit a more precise comparison of the alpha diversity in each forest (Krebs, 1999; Magurran, 2004). In addition, the number of unique species, the number and percentage of species represented by a single individual and the number of quadrats represented by more than 15 individuals in each forest were calculated. Curve estimation was performed to examine the relationships between the alpha diversity measures (y) and both DIF (x) and the relative basal area of *Shorea robusta* (x).

In order to assess Beta diversity, the ratio of number of woody species to the number of individuals found in each plot (species individual ratio) in each forest was calculated and regressed against DIF, and Jaccard's indices of similarity between the forests were calculated (Magurran, 2004). The relative ecological importance of each woody species was expressed using the importance value index (IVI) (Heikkinen & Birks, 1996; Galeano, Cediel & Pardo, 1998).

3.3 Methods (Studies III & IV)

In these studies the diversity and regeneration of woody species in two ecological niches – gaps and intact vegetation – were investigated. The gap attributes were assessed and their associations with diversity, dominance, and early growth of woody species were examined.

3.3.1 Gap and intact vegetation survey

These studies were based on both natural and artificial canopy gaps formed through whole tree fall. The artificial tree fall refers to selective felling carried out either by the Department of Forests or illegal loggers. A gap is defined as an open area larger than 25 m^2 created by the removal of canopy trees, in which most of the living plants are less than 5 m tall and less than 50% of the height of the surrounding canopy trees (Lawton & Putz, 1988). In the studies both 'canopy gaps' (the areas in gaps in which there is no canopy directly above the ground vegetation) and 'extended gaps' (the spaces enclosed by trees surrounding canopy gaps) were considered (Runkle, 1982). Areas with intact vegetation were defined as areas with ca. 100% closed canopy, as measured by a densiometer.

After field reconnaissance and visual interpretation of satellite images, six compass directions (20^o, 50^o, 110^o, 240^o, 250^o, and 320^o) were chosen and

transect belts were drawn on a satellite image. In order to cover the entire core zone of the forest, three arbitrary transect belts on either side of the East-West National highway were laid out from the midpoint of the highway. The highway and its midpoint were taken as a reference for gap and intact vegetation surveys since the highway divides the forest into two blocks. Arbitrary transect belts of 40 m width were laid out by five people walking 10 m apart from one another until both 10 gaps and intact vegetation spots had been encountered. Care was taken to ensure that spots in the intact vegetation were situated close to gaps (5-50 m away from a random border tree of each gap); hence topographical characteristics of the gap and corresponding non-gap areas were similar. A total of 60 gaps and intact vegetation spots, 10 spots per transect belt, were identified, labeled with paint on border trees and assigned serial numbers.

For each gap, its longest and perpendicular shortest axes were measured to calculate the gap area as an ellipse. Trees larger than 20 cm in dbh at the edge of each gap were identified to species level and their dbh was measured. The species, stump diameter, and state (alive or dead) of the gap makers (trees with $\geq$ 20 cm stump diameter creating a gap) were recorded. Mortality types (standing dead, trunk broken or uprooted), the causes of death and the decay of each gap maker in each gap were recorded. Gap age classes were estimated by visual comparison of the decay classes of gap makers and the decay classes of known log remains and stumps created by cutting in nearby areas (with the assistance of office records or people involved in logging operations). For gaps in which multiple trees had fallen, the oldest gap maker was designated as the key determinant of gap age and cause of tree fall since it was considered to be the primary creator of the gap (Zang & Wang, 2002). In order to avoid spatial autocorrelation and combined effects of adjacent gaps along the transect belts, a minimum distance of 100 m between successive border trees of sampled gaps was maintained.

3.3.2 Forest inventory

Detailed inventories in each gap and intact vegetation plot were carried out using 25 m^2 quadrats; one laid in the middle of each gap, where its two perpendicular axes intersected. For intact vegetation, the quadrats were placed at points where the densiometer showed complete canopy closure. Nested 4 m^2 quadrats were also laid out in each gap and intact vegetation plot at the corner of each 25 m^2 quadrat. Within the nested quadrats, all woody individuals with a height between 10 cm and 200 cm were identified to species level, counted and the collar diameter and height of the tallest seedlings were measured. Species were categorized as tree, shrub and herb.

Within the larger quadrat (25 m^2), individuals taller than 200 cm were identified to species level and their dbh was measured. Individuals were grouped into seedling (height between 10 cm and 200 cm) and sapling (taller than 200 cm).

3.3.3 Data analysis

The total number of species, number of individuals, species per individuals, and a variety of commonly used alpha diversity indices including Margalef's index of species richness, Shannon-Wiener index, Complement of Simpson's index, Shannon's measure of evenness and Fisher's index of diversity, were computed for each type of plot (Krebs, 1999; Magurran, 2004).

The plot-level density of each growth form and population density of important tree species were calculated and compared between the gaps and the intact vegetation using paired sample t-tests. Percentage values were calculated for each gap size class, number of tree falls, gap age, and tree fall causes (i.e. natural and artificial). Descriptive statistics were calculated for all variables used in the analyses. The mean gap sizes resulting from natural and artificial tree falls were compared using independent sample t-tests. Chi-square tests were used to test the significance of differences in frequencies of gaps created by single natural tree fall and those created by multiple tree falls and/or artificial causes. Gap attributes, i.e. gap areas, gap plot-level basal areas of fallen trees and border trees (trees remaining around the gap) were calculated and correlated with diversity measures and a variety of seedling growth parameters using Pearson correlation coefficients. Pearson correlation was also used to evaluate relationships among the measured gap parameters (i.e. gap area, fallen tree basal areas and number of tree falls).

For all studies, detailed forest inventories were carried out between October 2006 and March 2007. Species were identified *in situ* when possible, or by comparison with voucher specimens at the National Herbarium of Nepal. Prior to analyses, the data sets were normalized by log transformation and missing values were replaced by means as deemed necessary. All statistical analyses were performed using SPSS version 15 (SPSS for Windows, Chicago: SPSS Inc.).

'Without knowing it, we utilize hundreds of products each day that owe their origin to wild animals and plants. Indeed our welfare is intimately tied up with the welfare of wildlife. Well may conservationists proclaim that by saving the lives of wild species, we may be saving our own.' —Norman Myers

4 Results and discussion

4.1 Responses to a bundle of disturbance factors

4.1.1 Stand structure and advanced regeneration

Of the five forests studied, four showed an inverse relationship between the overall stand density and the diameter class, while the heavily disturbed forest (V) did not **(Fig. 6A)**. Such patterns of decreasing overall stem density with increasing diameter size class are typical of secondary dry tropical forests (González-Rivas *et al.*, 2006; Timilsina, Ross & Heinen, 2007). The low number of adult trees in the larger diameter classes in the least disturbed forests **(Fig. 6B)** could be related to the extraction of large trees for timber production; which was supported by a subsequent regression analysis showing an inverse linear relationship between the density of adult trees and DIF values ($r^2_{adj} = 0.81$; $p = 0.022$). However, the quadratic relationship between the density of adult trees and the diameter class in heavily disturbed forests **(Fig. 6B)** could be related to the amount of past illegal cutting in the lower diameter class (20-40 cm dbh). Trees of this size are often excessively felled due to their suitability for house construction and fuel-wood. Similar observations have been made in other tropical forests in India (Muthuramkumar *et al.*, 2006).

The quadratic relationship between the DIF values and overall stem density (i.e. density of saplings, poles and adult trees) showed higher stem density in moderately disturbed forests than in both the least and most heavily disturbed forests ($r^2_{adj} = 0.92$; $p = 0.040$). This pattern was also observed for the density of juveniles of the most dominant species, *S. robusta* ($r^2_{adj} = 0.91$; $p = 0.041$), indicating that mild disturbance supports species regeneration.

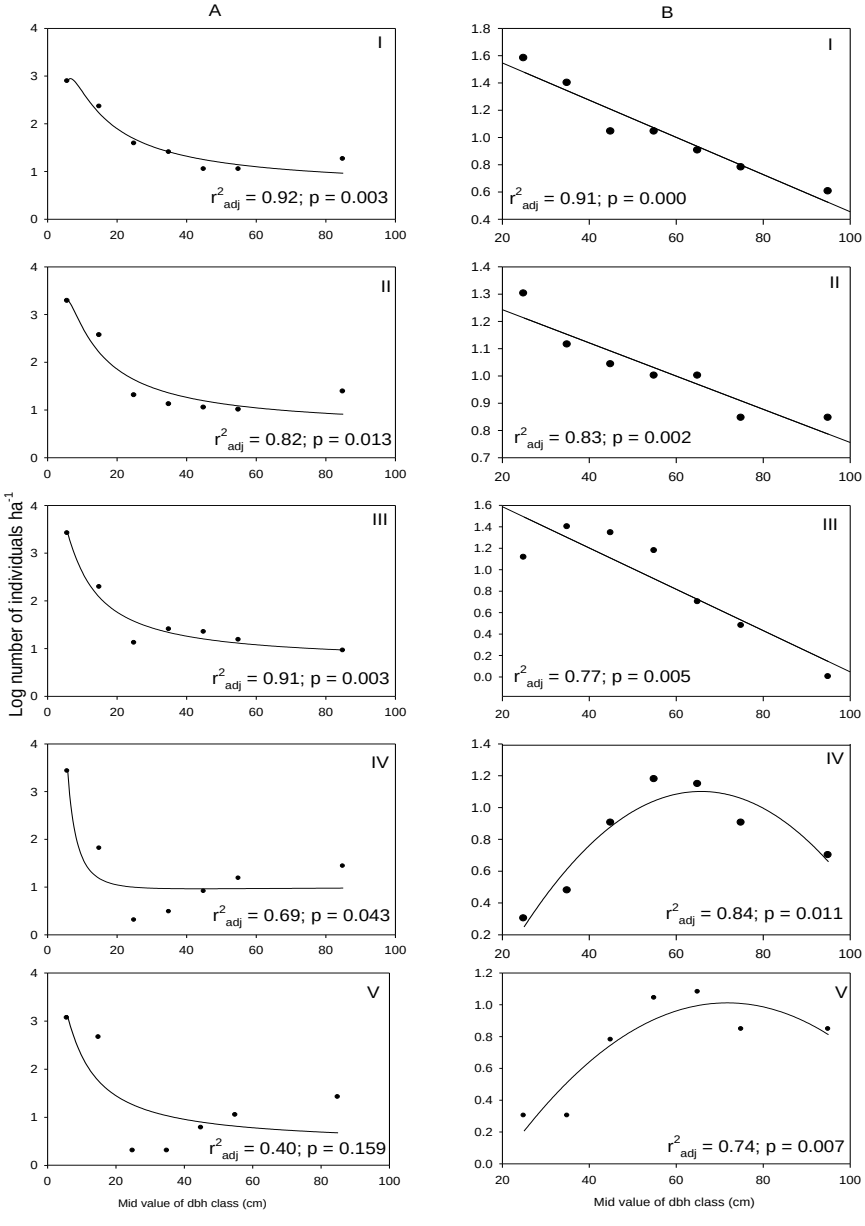


Figure 6. Relationships between mid-values of the dbh class and combined density of saplings, poles and adult trees (A) and density of adult trees alone (B). Roman numerals (I-V) represent the disturbance gradient from the least (I) to the most heavily disturbed forests (V).

The positive linear relationship between DIF and the single species occupancy of *S. robusta* found in this study (r^2_{adj} = 0.78; p = 0.028) is consistent with an earlier finding of Pandey and Shukla (2001), who recognized *S. robusta* to be a disturbance-tolerant species. However, the high population density of all species, including *S. robusta*, in moderately disturbed forests, could be attributed to a number of interacting factors. Firstly, vegetation cover in moderately disturbed forests may have been maintained by prolific ramet producers (e.g. *S. robusta*), particularly through rhizomes or root-stocks, as forest openings created by disturbance accelerate these processes (Jackson, 1994; Pandey & Shukla, 2001). Secondly, disturbance caused by past selective logging has created gaps in the stand (Sapkota & Oden, 2009; Sapkota, Tigabu & Odén, 2009), which generally increase light intensity and soil temperature, while reducing competition for water and nutrients, compared with undisturbed sites (Denslow, Aaron & Sanford, 1998). Thirdly, mega herbivores (e.g. rhinos, deer, cows, goats etc.) and dung beetles may facilitate seed dispersion, germination and growth of many tree species through defecation (Pradhan, Wegge & Moe, 2007). Following animal defecation, dung beetles have been frequently observed facilitating seed germination and seedling growth as they generally maintain a favorable micro-environment (Shepherd & Chapman, 1998). These factors may have occurred and interacted at optimum level in the forests subjected to mild disturbance, and therefore may have increased the population density of trees.

4.1.2 Species spatial patterns

Of the 14 species found in plots with two or more disturbance intensities, 10 showed changes in their dispersion patterns with changes in disturbance intensity **(Table 2)**. Disturbances often lead to changes in species' habitat conditions (Sagar, Raghubanshi & Singh, 2003) and competition (Rozas & Fernandez Prieto, 2000). The changing dispersion patterns of *Careya arborea* Roxb. and *Cassia fistula* Linn. from clumped to uniform are consistent with the findings of Sagar, Raghubanshi & Singh (2003), who observed a shift from clumped to uniform dispersion patterns associated with a change from higher to lower stem density. The dispersion pattern of *Adina cardifolia* Willd. ex Roxb. changed from clumped to random across the disturbance gradient, supporting the hypothesis that the occurrence of a random pattern is normally a result of transformation from an initially clumped pattern caused by self-thinning or some other disturbances (Rozas & Fernandez Prieto, 2000).

Table 2. Dispersion patterns (c = clumped; u = uniform; r = random) and abundance of species across the disturbance gradient computed based on a bundle of disturbances.

Species	Disturbance gradient				
	I	II	III	IV	V
Shorea robusta Gaertn f.	297^{c}	815^{c}	834^{c}	875^{r}	704^{c}
Lagerstroemia parviflora Roxb.	119^{c}	30^{u}	32^{c}	14^{u}	10^{c}
Symplocos spp.	25^{u}	16^{c}	14^{u}	82^{c}	8^{u}
Terminalia alata Heyne ex Roth.	35^{c}	19^{c}	45^{c}	37^{c}	
Semecarpus anacardium Linn.f.	35^{u}	15^{c}	62^{c}	22^{c}	
Eugenia operculata Roxb.		6^{u}	10^{c}	9^{u}	
Syzigium cumini Linn.		13^{u}	50^{c}		
Mallotus philippensis (Lam.) Muell.Arg.	58^{c}	67^{c}			
Adina cardifolia (Willd. ex Roxb.) Benth.	5^{c}		10^{r}		
Careya arborea Roxb.		13^{c}		6^{u}	
Pterospermum lanceaefolium Roxb.	6^{u}		8^{u}		
Sapium insigne Royle) Benth. ex Hook. f		10^{u}		17^{u}	
Cassia fistula Linn.		14^{c}		11^{u}	
Cornus oblonga Wall.			5^{r}	22^{c}	

The dispersion patterns of *S. robusta* and *L. parviflora* also changed with increasing disturbance intensity; however, in most cases they had a clumped distribution pattern. Clumped dispersion patterns of species with high abundance (e.g. *L. parviflora* and *S. robusta* in this study) may be related to resprouting ability (Sagar, Raghubanshi & Singh, 2003). As succession proceeds with some intervention, population spatial patterns shift from highly aggregated to more random or uniform patterns (He, Legendre & LaFrankie, 1997). The hypothesis linking species' distribution patterns to the combined effects of many biotic and abiotic disturbance factors (He, Legendre & LaFrankie, 1997; Rozas & Fernandez Prieto, 2000) may explain the changing dispersion patterns of *Semecarpus anacardium* L.f. and *S. cumini* from uniform to clumped, and that of *Cornus oblonga* Wall. from random to clumped with increasing disturbance observed in this study.

4.1.3 Advanced regeneration of locally preferred tree species

Comparisons between each possible independent forest pair identified significant variations in the density of saplings (advanced regeneration) for five of the seven commonly exploited tree species **(Table 3)**. All species, except *L. parviflora*, were absent in forest type V, which indicates that these species have been over-exploited and that their fitness may have declined. At some critical level of disturbance, species may gradually become rarer or even locally extinct (Daniels, Gadgil & Joshi, 1995;

Pandey & Shukla, 2001). In contrast, the advanced regeneration of most of the species analyzed was poor in the least disturbed forest (I). The population density of *T. alata* was significantly higher in moderately disturbed forests (forest types III and IV), compared to the other forests, which can be attributed to the species' high light demand (Jackson, 1994). Despite their high fodder value, the population densities of *S. cumini* and *Eugenia operculata* Roxb. were significantly higher in forest type III than in other forest types, which could be attributed to low wildlife or herbivore feeding pressures (wildlife and herbivores DIF = 3.5). In contrast, the population density of *S. cumini* was low in forest type IV, even though herbivore pressure was also low in this forest type (DIF = 1), possibly because of excessive fodder collection by local people, since the forest is managed by the State with relaxed protection. *S. cumini* has been considered a preferred fodder for some wild animals in similar forests of Nepal (Pradhan, Wegge & Moe, 2007), which could explain the low population density (or absence) of this species in other forests. It is possible that some herbivores, like rodents, also act as seed predators (Blate, Peart & Leighton, 1998). Forest type I had a significantly lower population density of *C. fistula* than forest types II and IV. The lower population of *C. fistula* in forest type I may reflect its slow germination and growth in undisturbed habitats due to deep seed dormancy (Jackson, 1994). Nevertheless, most of the species analyzed here showed poor regeneration in the least and most heavily disturbed forests; whereas regeneration of most species was favored in forests that had been subjected to moderate disturbance intensity.

Table 3. Sapling/pole density ha^{-1} of seven locally preferred tree species together with their uses (Fo, Fu, T and M refer to fodder, fuel-wood, timber and medicine, respectively) across the disturbance gradient computed based on a bundle of disturbances.

		Disturbance gradient				
Species	Uses	I	II	III	IV	V
Terminalia alata	Fo, Fu, T, M	192b	32a	432c	544c	0
Lagerstroemia parviflora	Fu, T, M	656b	176a	368b	224ab	160a
Syzigium cumini	Fo, Fu, T, M	0	112a	544b	32a	0
Adina cardifolia	Fu, T	48a	0	96a	0	0
Careya arborea	Fo, Fu, T, M	32a	0	32a	96a	0
Eugenia operculata	Fo, Fu, T, M	32c	96cd	128d	96c	0
Cassia fistula	Fu, M	32b	176c	48bc	176c	0

Forest types with different letters are significantly different at $p < 0.05$ based on pair-wise Mann-Whitney *U* tests.

4.1.4 Species diversity

A total of 67 species representing 60 genera and 37 families were recorded in all studied forests; however, there was a decreasing trend in stand-level species number along the disturbance gradient **(Table 4)**. The decrease in the total number of species along the disturbance gradient and small number of unique species in disturbed forests found here may reflect repeated exploitation pressure on several specific species (Sagar, Raghubanshi & Singh, 2003). Too much disturbance leads to the loss of late-successional species, while favoring fewer early successional and/or disturbance-tolerant species (Johnson & Miyanishi, 2007). The disappearance of some sensitive woody species at their recruitment stage has been commonly observed as a result of grazing and browsing pressure (Onaindia *et al.*, 2004). In this study, some species were represented by only a single individual, and such representation varied from 27 to 50% along the disturbance gradient **(Table 4)**. This finding is well comparable with Sagar , Raghubanshi & Singh (2003), who observed that 18 to 30% of species (> 30 cm circumference at breast height) were represented by a single individual in five Indian dry forests. The presence of a large number of species with only one individual in the least disturbed forests (I and II) compared to the other forests might be due to recruitment limitation. These species could also be pioneer species that only respond to major disturbances, not to small gaps (Brown & Whitmore, 1992).

Table 4. Diversity measures in seasonally dry *S. robusta* forests along the disturbance gradient computed based on a bundle of disturbances.

Diversity	Disturbance gradient				
Measures	I	II	III	IV	V
Total number of species	41	37[$]	28	22	10
Total number of families	27	23[*]	19	19	7
No. of unique species	16	11	2	2	4
No. of species with single individual	12	14	8	6	5
Percentage of species with single individual	30	38	29	27	50
No. of quadrats with > 15 individuals	1	14	22	8	1

[$] one unidentified species; [*] plus one unidentified family

The regression analyses revealed that more than 90% of the decline in alpha diversity measures across the disturbance gradient could be explained by the DIF **(Fig. 7A)**; this indicates that less disturbance promotes species diversity. A similar observation of a significant monotonic decline in species diversity with increasing frequency of experimental disturbances was made by Collins, Glenn & Gibson (1995). This is probably mainly

because forests subject to low levels of disturbance are also often subject to low level of species exploitation, which ensures higher resource availability (Sagar, Raghubanshi & Singh, 2003). The decline in all alpha diversity indices across the disturbance gradient is also associated with an increase in the dominance of a particular species, *S. robusta*, along the same gradient. This was supported by the finding of a third order negative relationship between the relative basal area of the most dominant species, *S. robusta*, and alpha diversity measures in this study **(Fig. 7B)**.

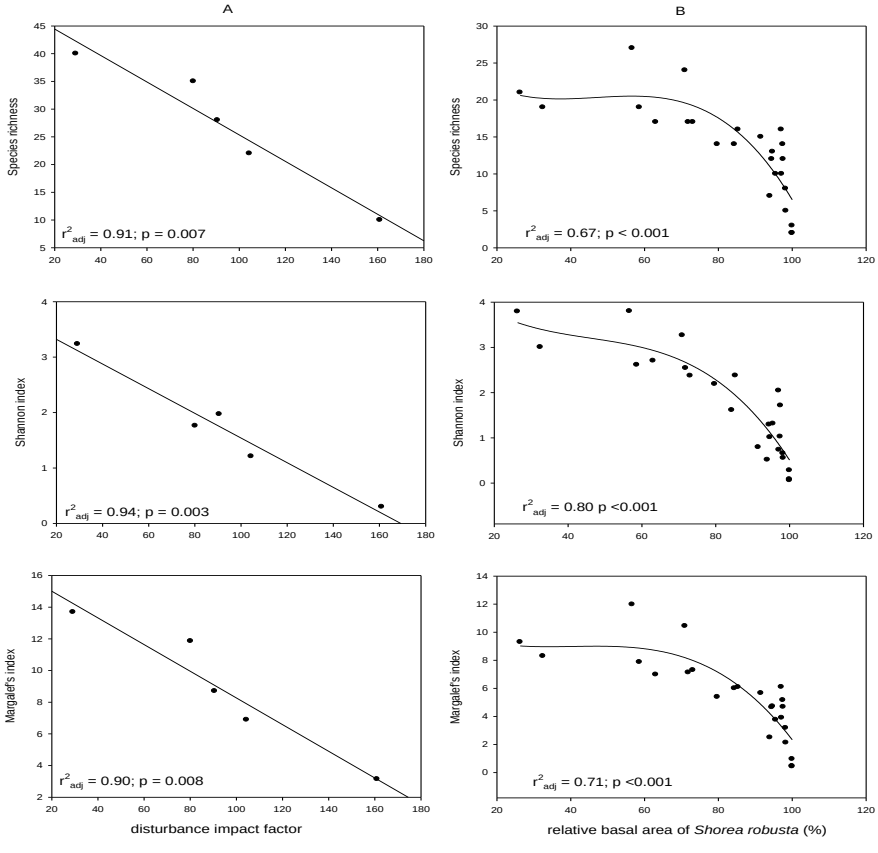


Figure 7. Relationships between various alpha diversity indices and disturbance impact factor (A); and the relative basal area of the dominant species (B).

The differences in number of species to number of individual ratios between forest types ($F_{[4,\ 20]} = 9.68$; $p < 0.0001$) indicate that the disturbance regimes affects the species richness and abundance in these

forests differentially, and hence influenced the Beta diversity (Magurran, 2004). This is further evidenced from the large Beta diversity between the least disturbed forest (I) and the most heavily disturbed (V), as evidenced by the low Jaccard's similarity index for these forest types (13.6%), while small Beta diversity between the two moderately disturbed forests, as evidenced by the high Jaccard's similarity index value (II and III; 56.3%). Sagar, Raghubanshi & Singh (2003) also found a positive relationship between Beta diversity and species:individual ratios. The decreasing trend of the species:individual ratio (numerical species richness) along the disturbance gradient **(Fig. 8A)** detected in the present study suggests that disturbances are a crucial factor affecting the inter-habitat diversity in Sal forest communities. It also indicates that species exploitation in the forests examined in this study is not homogeneous. Such phenomena may lead a species-rich forest to becoming a species-poor (Sagar & Singh, 2006).

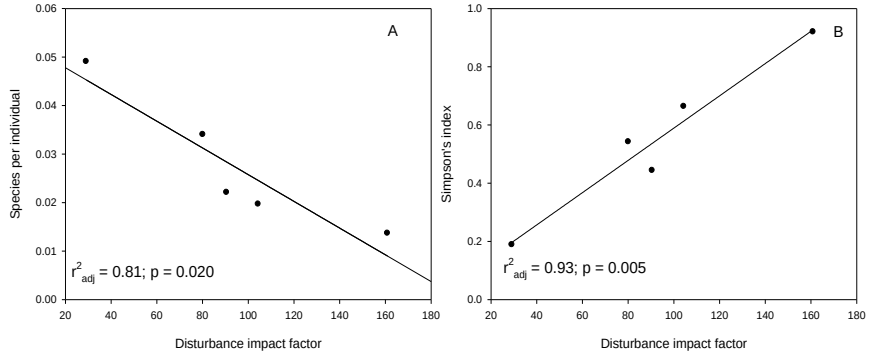


Figure 8. Relationships between DIF and numerical species richness (A); and dominance index (B).

4.1.5 Species importance and community dominance

Although *S. robusta* is dominant in all Sal forests, the extent of its dominance, as evidenced from its importance value index (IVI), differed considerably among the forests **(Table 5)**. Its IVI value was extremely high in the forest with high disturbance, confirming its ability to tolerate disturbance. Furthermore, Simpson's dominance index increased across the disturbance gradient **(Fig. 8B)**, indicating that the extent of single species dominance in the community increases with increasing disturbance magnitude; this is consistent with previous studies of forests in the Doon valley (Pande, 1999) and southern forests (Swamy *et al.*, 2000) of India. These phenomena could be related to the likelihood of *S. robusta* regenerating and establishing aggressively by suckers (Pandey & Shukla,

2001; Gautam & Devoe, 2006), which is strongly related to the level of seedling cutting, browsing and lopping. It has been argued that disturbance-led light availability speeds up seedling recruitment and establishment of *S. robusta* (Webb & Sah, 2003), largely due to its high light demanding nature (Jackson, 1994; Gautam & Devoe, 2006).

Table 5. Importance value index (IVI) for 15 tree species across the disturbance gradient computed based on a bundle of disturbances.

Family	Species	Disturbance gradient				
		I	II	III	IV	V
Dipterocarpaceae	*S. robusta* Gaertn f.	111	179	165	217	274
Lythraceae	*L. parviflora* Roxb.	35	13	11	5	8
Combretaceae	*T. alata* Heyne ex Roth.	18	13	22	14	-
Euphorbiaceae	*M. philippensis* Lam.	17	21	-	-	3
Anacardiaceae	*S. anacardium* Linn.f.	13	7	19	7	1
Combretaceae	*A. latifolius* Roxb. ex DC.	13	-	-	-	-
Leguminosae	*D. oojeinense* Roxb.	11	-	-	-	-
Sapindaceae	*S. oleosa* (Lour.) Oken	10	-	-	-	-
Cyperaceae	*M. sumatrensis* (Retz.) A.R.	8	-	-	-	-
Symplocaceae	*Symplocos* spp.	7	5	4	23	7
Anacardiaceae	*S. cytheria* Sonn.	-	11	-	-	-
Rubiaceae	*A. cadamba* Roxb.	-	11	-	-	-
Myrtaceae	*S. cumini* Linn.	-	7	14	-	-
Rubiaceae	*W. coriacea* (Wall.) DC.	-	-	25	-	-
Anacardiaceae	*Semecarpus* spp.	-	-	15	-	-

Repeated exploitation of some species, such as *T. alata*, *A. cardifolia*, *T. bellirica*, *S. cumini*, *E. operculata* and *C. arborea*, for fodder and fuel-wood in these forests alter the course of succession (pers. obs.), and thus may result in the forests becoming single-species dominated systems. The occurrence of different co-dominant species along a disturbance gradient can be attributed to their ability to tolerate competition for space and resources from *S. robusta* and the choice and extent of exploitation of the co-dominants by the local people. For example, *Wendlandia coriacea* (Wall.) DC. and *Symplocos* spp. are co-dominant species in relatively disturbed forests because they are the least preferred species by local people.

4.2 Responses to a single disturbance factor: tree fall gaps

4.2.1 Species diversity

The various diversity measures calculated for all growth forms together did not vary consistently between the gaps and intact vegetation areas **(Table 6)**. The total number of species (S) was slightly higher in the gaps than in the intact vegetation environments. A similar pattern was found for estimated species richness using Margalef's index (D_{Mg}). Irrespective of growth form, the total number of individuals (N) was higher in the gaps than in the intact vegetation. The species turnover rate, as measured by numerical species richness (S_c/N), was higher in the intact vegetation. The Shannon-Wiener index (H′), the complement of Simpson's index (1–D) and Shannon's measure of evenness (*J'*) were all slightly higher in the intact vegetation than in the gaps. However, Fisher's α diversity index (the most stringent measure of Alpha diversity) revealed that species diversity is higher in the gaps than in the intact vegetation.

Table 6. Species diversity indices of all growth forms combined in gaps and intact vegetation.

Diversity indices	Gap	Intact
No. of species	43	37
Margalef's index	5.39	5.00
Total No. of individuals	2414	1627
Numerical species richness	0.018	0.022
Shannon-Wiener index	2.066	2.502
Complement of Simpson's index	0.515	0.601
Shannon's measure of evenness	0.55	0.69
Fisher's α diversity index	21.65	19.02

The pattern of higher species richness in the gaps than in the intact vegetation is consistent with previous studies (Runkle, 1982; Denslow, 1995; Zang & Wang, 2002; Li, Bogaert & Nijs, 2005). Generally, gaps promote high species diversity by providing colonization sites for shade intolerant and pioneer species in the community (Clarke & Allaway, 1993; Dalling, Hubbell & Silvera, 1998) and by increasing their establishment and density, which in turn can lead to higher species richness (Denslow, 1995). Tree fall gaps generally cause environmental heterogeneity, with variations in light, temperature, moisture and/or nutrient regimes that trigger the germination and growth of several species (Denslow, 1995). In some cases, the increase in diversity caused by gaps may simply be a

transient effect of increased density and may disappear following thinning (Denslow, 1995; Gotelli & Graves, 1996; Hubbell *et al.*, 1999; Stevens & Carson, 1999). Therefore, the high number of individuals in gaps could also explain the slight increase in overall diversity (Fisher's index in particular) in gaps observed in the studies.

4.2.2 Stand regeneration

Seedling regeneration differed significantly between the gap and intact vegetation environments with regard to the growth-form spectrum. The results showed that seedling density was higher in the gaps than in the intact vegetation for both tree (Gap vs. Intact: 871 ± 33 vs. 578 ± 28 per 100 m^2; $t_{[59]} = 6.45$; $p < 0.0001$) and shrub species (Gap vs. Intact: 150 ± 13 vs. 93 ± 9 per 100 m^2; $t_{[59]} = 3.71$; $p < 0.0001$). These results are consistent with the findings of Bertrand *et al.* (1995) in desert habitats, Chambers (1995) in alpine tundra, and Whitmore (1989) in tropical rain forests. Generally, regeneration processes in gaps depend on several physical and biological factors (Arriaga, 2000). Canopy gaps always have higher light intensities at the soil surface, and hence often higher soil temperatures, than areas with closed vegetation (Denslow, Aaron & Sanford, 1998). Moreover, competition for one or more resources (e.g. light, nutrients, and water) is lower in canopy gaps than in intact vegetation environments (Bullock, 2000). Thus, the combined effects of increased light intensity, increased soil temperature and reduced competition increases seedling recruitment and establishment in canopy gaps compared to areas with closed canopies. Rapid recruitment of pioneer shrubs following gap formation is another important factor contributing to high seedling density in canopy gaps (Deb & Sundriyal, 2007). This was exemplified by *Clerodendron viscosum*, – a nurse shrub that promotes the regeneration of *S. robusta*, – that was found in substantially higher density in canopy gaps than in intact vegetation environments (98 vs. 45 individuals per 100 m^2). The lack of significant variation in herb density between the gaps and intact vegetation (Gap vs. Intact: 87 ± 9 vs. 75 ± 5 per 100 m^2; $t_{[59]} = 1.31$; $p = 0.193$) could be related to reduced availability of light due to overshadowing by the dense population of shrubs and trees, as well as competition for resources (Yu *et al.*, 2006).

4.2.3 Regeneration of locally preferred tree species

With regard to the socially preferred tree species, higher seedling density of *S. robusta* (Gap vs. Intact: 595 ± 32 vs. 362 ± 23 per 100 m^2; $t_{[59]} = 5.9$; $p < 0.001$) and *T. alata* (Gap vs. Intact: 38 ± 2 vs. 18 ± 1 per 100 m^2; $t_{[59]} = 9.8$; $p < 0.001$) were observed in the gaps than in the intact vegetation

environments. High prevalence of their seedlings in the gaps could support the hypothesis that the vegetation cover in disturbed sites (gaps) is maintained either by prolific ramet producers, especially through rhizomes and resprouts, or by strong light demanders, especially at the recruitment stage. This may be because the disturbance-led openings accelerate both regeneration processes (Pandey & Shukla, 2001). *S. robusta* is a prolific resprouter, but its resprouts develop more slowly in shaded than in open environments, hence their survival rates are lower under closed canopies (Rautiainen & Suoheimo, 1997). Similarly, the germination of *T. alata* (a strong light demanding species), is likely to be successful in exposed sites, provided soil moisture is available (Sen, Johri & Bisht, 2008). Furthermore, its seedlings are tolerant of continuous light and/or dry conditions due to their deep root systems (Sen, Johri & Bisht, 2008). However, since it provides good fodder, this species often faces repeated exploitation pressure following its recruitment (Upadhyay, 1992; Khanna, Pacholi & Singh, 1998). In contrast, significantly higher seedling densities of some shade-tolerant species (Jackson, 1994), such as *T. bellirica* (Gap vs. Intact: 17 ± 0.5 vs. 31 ± 1 per 100 m^2; $t_{[59]} = 17.7$; $p < 0.001$) and *Syzigium cumini* (Gap vs. Intact: 32 ± 1 vs. 72 ± 8 per 100 m^2; $t_{[59]} = 5.2$; $p < 0.001$), in intact vegetation environments could be related to the pre-gap canopy trees. Before gap creation, canopy trees might have shaded the micro-sites and maintained relatively even seedling distribution of shade-tolerant species (Uhl *et al.*, 1988). However, following gap creation, the microclimate might have changed considerably (Whitmore, 1996), thus reducing the survival rate of such species in the gaps, compared to the areas with intact vegetation.

4.3 Gap plot characteristics

The total number of dead trees that apparently created the examined gaps was 97; of which 56%, 30% and 14% were dead-standing, cut and windfalls, respectively. Gap size varied between 67 and 1418 m^2, with a median area of 216 m^2. Of the total number of gaps identified, almost 50% were of medium size (200 – 400 m^2), while large gaps (> 600 m^2) accounted for less than 10%. The number of gaps resulting from a single tree fall was more than double the number formed by two or more tree falls. Furthermore, almost 50% of the gaps were 10-15 years old, while only 5% were 15-20 years old. In addition, gaps resulting from natural causes were far more frequent (75%) than those formed by artificial tree falls (25%).

The range in gap area observed in here was similar to ranges recorded in studies in north east India (Barik *et al.*, 1992; Arunachalam &

Arunachalam, 2000) and central Japan (Yamamoto, 1995). Although many previous studies have found that gap size is correlated with the number of tree falls (Lima & Moura, 2008), the results here do not support such a relationship ($r = -0.049$; $N = 60$; $p = 0.707$). Instead, the finding is consistent with a study from north-eastern Mexico concluding that the number of tree falls does not necessarily explain gap size (Arriaga, 2000). However, the positive correlations observed between the basal area of the fallen trees and both their number ($r = 0.420$; $N= 60$; $p = 0.001$) and gap size ($r = 0.269$; $N = 60$ $p = 0.038$) were consistent with observations from studies performed in Atlantic Montane rainforests (Lima & Moura, 2008) and Nouragues, French Guiana (Van Der Meer & Bongers, 1996). These relationships may be linked to the cause, size, and number of tree falls during gap formation.

The gaps formed by artificially felled trees were significantly larger (375 ± 66 m^2) than those created by natural tree falls (260 ± 31 m^2) ($t_{[58]} = 3.8$; $p = 0.05$), as large trees are normally logged to maximize timber production (Gagnon *et al.*, 2004). In addition, logging operations may knock down additional trees during the felling process (Chandrashekara & Ramakrishnan, 1994; Lima & Moura, 2008). Therefore, logging operations may have caused the large gaps observed in this study, in which most of the trees that had been felled were large single or multiple trees.

4.4 Association between gaps and vegetation characteristics

Species richness had significant negative associations with both gap size and the basal area of bordering trees (**Table 7**), possibly due to the marked changes in microclimate that may occur with increases in gap size (Whitmore, 1996) and reduce the survival and growth of recruits, particularly in dry forests. However, increases in the Shannon index and Evenness with increasing tree fall basal area (**Table 7**) suggests that more space was available for early colonizers to invade in the new habitats created after large trees had fallen, as noted by Li, Bogaert & Nijs (200w5). Before gap creation, these trees might have shaded wider micro-sites and maintained a relatively even distribution of non-pioneer species (Uhl *et al.*, 1988), leading to higher Evenness and Shannon indices. The majority of the species studied here (ca. two-thirds of those examined) appeared to be shade tolerant, which supports this hypothesis.

The increase in the basal area of fallen trees was associated with reductions in Simpson's index of dominance and the relative seedling density of *S.*

robusta **(Table 7)**. This suggests that the single-event gaps created by the fall of large and/or multiple gap makers may lower the dominance of *S. robusta*. This reduction may be attributed to the typical ephemeral seedling stock of this species, as observed in other members of the dipterocarpaceae (Rosario, 1982). Dipterocarps may be adversely affected by shocks caused by sudden exposure to sunlight, which are often coupled with wind factors (Rosario, 1982). Furthermore, dipterocarps require partial shade between their germination and pole stages, while they require increasing amounts of light as they mature (Mauricio, 1985). Therefore, the natural regeneration of dipterocarps is likely to be most efficient in relatively small gap environments, which provide partial light and wind shelter (Tuomela *et al.*, 1996).

Table 7. Correlations (r) between gap plot characteristics and vegetation attributes (N = 60). BA refers to basal area.

	Gap plot characteristics		
Vegetation attributes	Gap Area (log_{10})	Border BA	Tree fall BA
Species richness	-0.287*	-0.463**	0.037
Shannon index	-0.086	-0.218	0.259*
Evenness	0.086	-0.051	0.280*
Simpson's index	-0.060	0.010	-0.270*
Relative seedling density of *S. robusta*	-0.153	-0.029	-0.358*
Seedling height (H)	0.074	0.006	-0.114
Seedling collar diameter (D)	0.035	0.042	0.141
H/D ratio	0.025	-0.057	-0.272*
Average sapling dbh	-0.251*	-0.386**	0.105
Plot level sapling BA	-0.244	-0.356**	0.059

**, * p values <0.01, <0.05, respectively

The negative relationship between the height-to-diameter ratio of the tallest seedling and basal area of the fallen trees **(Table 7)** found here may indicate that gaps caused by multiple falls of large trees favor the radial growth of seedlings over their height growth. These findings concord with the results of a study performed in Indonesia (Tuomela *et al.*, 1996), where a negative relationship was observed between seedling height and gap size. This relationship may be attributable to gap-size related differences in the seedlings' access to and/or competition for light (Dekker, Van Breugel & Sterck, 2007). Seedlings in larger gaps often have continuous access to light, leading to relatively weak competition among individuals for light and space. Therefore, a higher investment in radial stem growth at the cost

of height gain may occur (Sterck & Bonger, 1998) as light is almost equally available to all individuals. Similar relationships have been observed in Ghana (Doland Nichols *et al.*, 1998) and the Netherlands (Dekker, Van Breugel & Sterck, 2007).

The negative relationship between gap area and average sapling dbh found in this study **(Table 7)** corroborated results of an earlier study in Indonesia, which found a negative effect of larger gaps on seedling growth (Tuomela *et al.*, 1996). Higher light availability in large gaps often increases plant resources for a certain period after gap creation, and the high resultant plant growth increases resources for herbivores and predators. Consequently, populations of herbivores and predators that feed on plants and young leaves (Richards & Coley, 2007) may increase and ultimately reduce the rates of seedling survival and growth in larger gaps (Brokaw, 1985). Similarly, the negative relationships between the border tree basal area of gaps and both sapling dbh and plot-level basal area can be attributed to effects of pests (Richards & Coley, 2007) and/or root competition between the border trees and saplings (Brokaw, 1985). For instance, Bylund (1997) and Sapkota, Tigabu & Odén (2009) demonstrated that old-growth forests containing large trees often serve as host trees for various herbivores (e.g. ants, termites and grasshoppers; pers. obs.), which feed on the young leaves of seedlings and hence cause reductions in current saplings' growth and size. Root competition for nutrients and water between the seedlings and bordering trees might also contribute to reduction in seedling growth and survival.

We got rich by violating one of the central tenets of economics: you shall not sell off your capital and call it income. And yet over the past years we have clear-cut the forests, fished rivers and oceans to the brink of extinction and siphoned oil from the earth as if it possessed an infinite supply. We've sold off our planet's natural capital and called it income. And now the earth, like the economy, is stripped. —Kalle Lasn

5 Conclusion and recommendations

Studies I and II showed that advanced regeneration, diversity and spatial patterns of tree species in the Sal forests clearly respond to a bundle of inherent disturbances. The total stem density of saplings and poles increased as the intensity of the bundle of disturbance factors increased to a certain level, while most of the tree species in the community showed fluctuating dispersion patterns across the disturbance gradient. The regeneration of important tree species such as *S. robusta*, *T. alata*, *S. cumini*, *E. operculata* and *C. fistula* exhibited differential responses to disturbance. As a whole, regeneration was favored in forests subjected to moderate level of disturbance. Therefore, moderate disturbance intensity not only promotes high stand density, but also enhances the regeneration of locally preferred tree species and affects their dispersion patterns. High disturbance intensity appears to favor single species dominance of *S. robusta*, and in turn, lowers tree species diversity. A follow-up investigation showed that the changes in tree diversity are related to the relative basal area of the dominant tree species.

Studies III and IV showed that tree fall gap – a single disturbance factor – favors species regeneration, and results in higher seedling density of some socially preferred tree species, including Sal. By increasing seedling density, gaps also maintain species diversity. However, increases in gap size do not seem to enhance the overall species diversity, regeneration and seedling growth. Hence species diversity and regeneration in gaps may be more closely correlated with the process of gap origin than to the size of the gap. Similarly, the basal area of fallen trees is positively associated with species diversity, but the presence of large living trees around gaps tends to reduce species richness, regeneration and seedling growth.

Theoretical outlook and management implications:

In accordance with the proposed conceptual framework, the mixed effects of multiple disturbance regimes on regeneration and diversity in Sal forests were explored in the studies underlying this thesis. A number of indicators linked to diversity and regeneration in Sal forests seemed to respond to a bundle of disturbances differentially. The overall stand density of the young population and the population density of important tree species (including Sal) responded positively to the disturbances to some extent, while diversity measures responded negatively. In addition, the bundle of disturbances altered the distribution patterns of most of the species studied here. A single disturbance factor – tree fall gap – also had mixed effects on species diversity and regeneration. Canopy gaps enhanced a number of regeneration parameters and diversity measures (e.g. Fisher's α); while a number of vegetation attributes responded negatively. Similarly, the regeneration performance of some species benefitted from the creation of canopy gaps. Generally, four important points can be drawn from these studies: (i) the diversity, regeneration and early growth of Sal forest communities respond sufficiently well to both bundle of disturbance regimes and to a single disturbance factor; (ii) some regeneration and diversity attributes are adversely affected and some are enhanced by both the bundle of disturbance regimes and tree fall gaps; (iii) the degree of these effects (positive and negative) in the Sal forest stands depends on the intensity of the disturbance factors; and (iv) neither the most severe disturbance nor the least severe disturbance promotes species regeneration and diversity of Sal forests.

These findings are in accordance with the Intermediate Disturbance Hypothesis, which postulates that moderate disturbance intensity maintains ecosystem integrity more effectively than higher or lower disturbance intensity (Connell, 1978; Pandey & Shukla, 2001; Haeussler *et al.*, 2002). This is probably because over-exploitation of tree species for timber, fodder, fuel-wood and non-timber forest products by local people, and extreme browsing, trampling and uprooting by herbivores may impede the regeneration process in heavily disturbed sites. In contrast, reduction in light intensity and soil temperature, and increased competition for water and nutrients due to limited gap creation could account for the poor regeneration or lack of regeneration of most species in the least disturbed forests.

On the contrary, the high regeneration stock in the forests with intermediate levels of disturbance should be considered from the perspectives of both the Intermediate Disturbance Hypothesis and the regeneration strategy of the

dominant tree species, such as Sal. This is because a bundle of mild disturbances accelerate the regeneration process of Sal (and hence favor high levels of Sal regeneration stock) due to the species' ability to regenerate aggressively via suckers from disturbed trees and its strong light requirements. Therefore, the disturbance regimes can be seen as a potential management tool for Sal forests since it provides opportunities for Sal to regenerate vegetatively through the root suckers of disturbed trees that receive sufficient light through tree fall disturbance. However, as the single species dominance of Sal in the forests with high disturbance confirms, this species has high disturbance tolerance and the extent of single species dominance in Sal forests increases with increasing disturbance intensity. Taking the present forest type and their current socio-economic situations into account, the following management implications can be drawn:

1. Mild disturbance with limited public and herbivore access to the forests does not necessarily hinder the overall stand regeneration and species diversity, and may enhance them.
2. Since the rural population is highly dependent on these forests for their subsistence needs, strict protection of these forests is not feasible.
3. Ecosystem-based management, focusing simultaneously on optimization of the consumptive forest products for human populations and enhancement of species' regeneration and diversity, would be a viable management strategy for Sal forests.
4. Special attention should be paid to the intensity of forest use and extraction of forest products, since heavy disturbance was found to be detrimental to the regeneration and diversity of the forests.

Future research priorities:

In Studies I and II, the type and intensity of varying inherent disturbances were identified, assessed and collectively considered in a bundle, and their synergistic effects on species diversity and regeneration were investigated. However, none of the studies provided empirical answers to the following questions. What types of disturbance are most often experienced by different species of the Sal forest community, and at what stage of the regeneration process do they experience these disturbances? Studies addressing these questions will have direct relevance to ecosystem-based forest management strategies, and extensive consideration of possible ecological responses to the different types of inherent disturbances outlined in this thesis is warranted. Such research should be given priority in the future in order to predict possible future changes in the species composition of Sal forests.

In Studies III and IV, the gap characteristics were assessed and linked to regeneration, diversity and dominance in gaps. This work also focused on differences between gaps created by different causes: selective logging vs. natural tree fall, single tree fall vs. multiple tree falls. However, there was no analysis of the linkages between the origin and intensity of gap creation for a number of forest species. Therefore, this aspect should also be a future research priority in order to elucidate how individual species responds to the creation of gaps by different mechanisms and likely changes in forest composition if selective logging becomes more intense, less intense or continues at the same level.

'He (modern man) commonly thinks of himself as having been here since the beginning — older than the crab — and he also likes to think he's destined to stay to the bitter end. Actually, he's a late comer, and there are moments when he shows every sign of being an early leaver, a patron who bows out after a few gaudy and memorable scenes.' — E.B. White

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'Birth, life, and death - each took place on the hidden side of a leaf.' —Toni Morrison

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नेपाली सारंश (Nepali summary)

नेपालको साल वनभित्र रहेका प्रजाति विविधता, पुनरुत्पादन र प्रारंभिक वृद्धि : स्वभाविक प्रकृतिका वन विघ्नवाधाहरु प्रतिका प्रतिक्रियाहरु

सार-संक्षेप

धेरै बर्षदेखि वनमा हुनेगरेका विघ्नवाधाहरु गहन अनुसन्धानको बिषय रहीआएको छ । परन्तु, विशेषगरी सालका वनहरुमा हुनेगरेका विविध किसिमका विघ्नवाधाहरु र यसले सो वनभित्र पाइने वनस्पतिहरुमा पार्ने गरेको योगात्मक प्रभावको बारेमा प्रयाप्त अभिलेखहरु छैनन् । त्यसैले, पांच वटा नेपाली साल वनहरुमा गरीएको विस्तृत वन मापनबाट प्राप्त तथ्यांकलाई केलाउँदै र विविध प्रकारका वन विघ्नवाधाहरुको तीव्रतालाई एउटा समष्टिगत रुपको 'एकमुष्ट विघ्नवाधा' मा रुपान्तरण गर्दै, यो शोधपत्रले 'वन विघ्नवाधा - प्रजाति विविधता/पुनरुत्पादन सम्बन्ध' लाई उजागर गरेको छ । संगसंगै, यसले एकल वन विघ्नवाधा - प्राकृतिक तथा मानवीय कारणहरुले रुखहरु नासीई वन छत्रमा देखिने रिक्तता - र सोको प्रजातिको विविधता, पुनरुत्पादन तथा प्रारंभिक वृद्धिमा पर्न सक्ने प्रभावहरुको पनि अध्ययन गरेको छ । स्वभाविक प्रकृतिका विविध वन विघ्नवाधाहरुको तीव्रतालाई समाहित गरी बनाइएको 'एकमुष्ट विघ्नवाधा' र यसको तीब्रताको प्रभाव वनस्पतिका विविध पक्षहरुमा फरक फरक ढंगले परेको पाइयो । वन विघ्नवाधाको तीब्रतामा केहि हदसम्म वृद्धि हुँदा वनमा स्थापित पुनरुत्पादनको कुल संख्यामा वृद्धि भएको पाइयो । वन विघ्नवाधाको तीब्रतामा परिवर्तन आउँदा अधिकांश रुखका प्रजातिहरुले आफ्नो वनभित्र छरिएर रहने प्रवृतिमा पनि परिवर्तन देखाए । मध्यम स्तरको विघ्नवाधा भएको वनमा अधिकांश सामाजिक महत्व बोकेका रुखका प्रजातिहरूको पुनरुत्पादन उच्च देखियो । एकल वन विघ्नवाधामा (छत्र रिक्तता) मात्रै केन्द्रित विश्लेषणबाट प्राप्त नतिजा अनुसार, छनौट गरी हटाइएको रुखको कारणले बनेका छत्र रिक्तताले केहि सामाजिक महत्व बोकेका प्रजातिहरुका (साल समेत) विरुवाको संख्यामा वृद्धि गर्नुका साथै प्रजाति विविधतामा समेत सहयोग गरेको देखियो । यध्यपी, प्रजाति विविधता र पुनरुत्पादनको छत्र रिक्तताको क्षेत्रफलसंग सकारात्मक पारस्परिक सम्बन्ध नदेखिएबाट, छत्र रिक्तता मुनि कायम प्रजाति विविधता र उच्च पुनरुत्पादन, सोको क्षेत्रफल भन्दा अन्य विविध पक्षहरुसंग सम्बन्धित रहेको पाईयो । साधारणतया, मध्यम स्तरको विघ्नवाधा भएको वनले प्रजाति विविधता तथा पुनरुत्पादन कायम गर्दछ, जसलाई सोही वनमा पाइने मुख्य प्रजातिको पुनरुत्पादन गर्ने रणनीतिले थप वल प्रदान गर्दछ । यसरी, यहाँ देखाइएका नतिजाहरुले 'मध्यम वन विघ्नवाधा' र 'वीज विरुवाको सिमितता' संग सम्बन्धित परिकल्पनाहरुलाई आत्मसात गरेको छ । निष्कर्षमा, साल वन व्यवस्थापनको निम्ति मध्यम स्तरको वन विघ्नवाधा प्रयोगयोग्य साधन हुन सक्दछ ।

मूळ शब्दहरु: छत्र रिक्तता, वन विघ्नवाधा, मध्यम विघ्नवाधा परिकल्पना, विविध विघ्नवाधाहरु, वीज विरुवाको सिमितता परिकल्पना, शोरिया रबुश्टा